OVIPOSITION BEHAVIOUR IN THE DART-TAILED WASP, *CAMERONELLA* DALLA TORRE (HYMENOPTERA: PTEROMALIDAE: COLOTRECHINAE)

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Abstract

The first description of oviposition behaviour by a dart-tailed wasp, *Cameronella* Dalla Torre, 1897, is provided based on observations and a video recording of an adult female attempting to oviposit into a gall of *Apiomorpha ovicola* (Schrader, 1863). The oviposition behaviour of the female of *Cameronella* is similar to that of other pteromalids that have an expended ovipositor. Three major behaviours associated with oviposition were observed: antennation (including at the orifice of the host's gall), drilling and preening.

Introduction

Dart-tailed wasps, *Cameronella* Dalla Torre, 1897, are endemic to Australia and are specific parasitoids of the gall-inducing scale insect *Apiomorpha* Rübsaamen, 1894 (Hemiptera: Eriococcidae) (Boucek 1988). The common name of the wasp is derived from the modified epipygium of the adult female, which resembles the tail of a dart although it is more similar to the straight fletching of an arrow, in that there are only three vanes (Fig. 1). These wasps are rarely caught by hand-netting or Malaise traps and are poorly represented in collections. For example, the Australian National Insect Collection has 48 specimens, the South Australia Museum has three specimens and the Queensland Department of Agriculture, Fisheries and Forestry has only two specimens. Seven described species were listed by Boucek (1988) but he suggested that only three might be valid. Because only a few of the specimens in museum collections have been identified to species, it is difficult to identify any recently collected specimens to species.

In accord with the rarity of specimens, the biology and ecology of *Cameronella* are little known. We determined that *Cameronella* is an ectoparasitoid, because early stage larvae were found attached externally to the cuticles of females of *Apiomorpha* extracted from galls (Wang *et al.* unpublished). The biology of the other 11 Australian genera of Colotrechninae (Boucek 1988) is even less known. Six associate with unidentified galls on *Eucalyptus* and *Casuarina* or with twig-boring beetles, while nothing is known of the other five genera (Boucek 1988).

Oviposition behaviour of pteromalids has rarely been described. Both *Cheiropachus quadrum* (Fabricius, 1787) and *Anisopteromalus calandrae* (Howard, 1881) are pteromaline parasitoids attacking larvae of small beetles (olive bark beetle and bruchid beetle). Their oviposition behaviours have been described as host searching, antennation, drilling, piercing and inserting, oviposition, preening and, sometimes, feeding on host body fluids (Fig. 2) (Carlos *et al.* 1999, Begum 1995). The oviposition of the well-studied genus

Nasonia Ashmead, 1904 (Pteromalinae) on fly puparia has also been described and, based on observations by Edwards (1954) and others (*e.g.* Girault and Sanders 1910, Altson 1920, Jacobi 1939), includes the same behaviours as *Ch. quadrum* and *An. calandrae*. However, all of these differ from *Cameronella* in that they lack extended ovipositors.

Fig. 1. An adult female of *Cameronella* sp. (above) and the "dart tail" of another adult female of *Cameronella* (below), both from Western Australia.

Oviposition behaviour of pteromalids with extended ovipositors has been less well described. Oviposition in one fig-wasp parasitoid group, *Apocrypta* Coquerel (Sycoryctinae), was described by Ulenberg and Nübel (1982) and Zhen *et al.* (2005), who focused mainly on abdominal movements during

drilling. Oviposition was simply described as consisting of three phases: searching for a receptive host, penetrating the host and oviposition before withdrawing the ovipositor (Zhen *et al.* 2005). This is similar to the process described for other pteromalids but lacks feeding on the host. Female wasps with expended ovipositors often need to drill through thick plant tissue to get to the host. Consequently, the female is unable to reach the host with her mouthparts and cannot feed on host body fluids. Species of *Apiomorpha* live within tough woody galls on their eucalypt hosts and thus we expected *Cameronella* would have similar oviposition behaviour to that of *Apocrypta*.

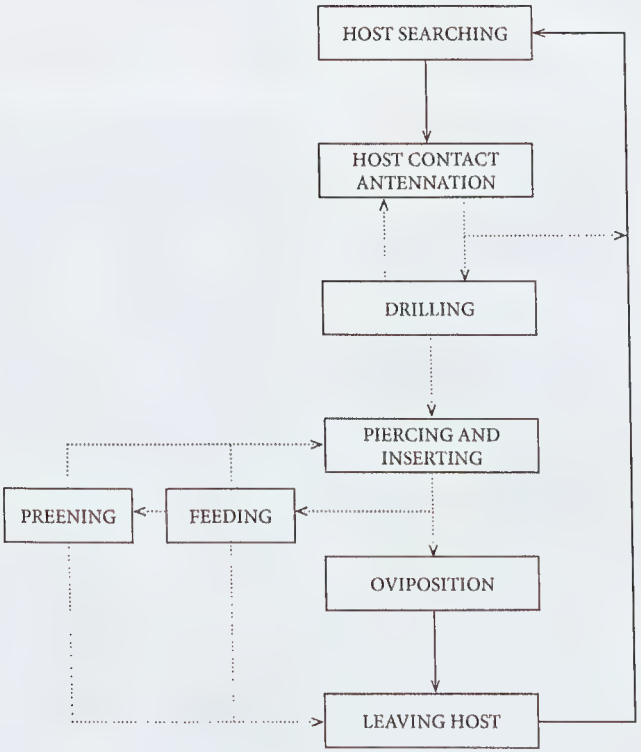

Fig. 2. Flow chart of the oviposition behaviours of females of *Cheiropachus quadrum* (Pteromalidae: Pteromalinae), from locating the host and ovipositing, through to leaving the host. Solid lines indicate invariable paths and dotted lines indicate alternative pathways. (After Carlos *et al.* 1999).

Methods

All observations were carried out at The University of Queensland, St Lucia, Brisbane. The adult female of *Cameronella* sp. observed ovipositing was reared from *Apiomorpha ovicola* (Schrader, 1863) collected by P. J. Mills from *Eucalyptus microcarpa* (Maiden) Maiden at Dimboola, Victoria on 9 July 2011. The female wasp emerged 53 days after the gall was collected and was kept in a plastic box and fed with honey solution.

The 7-day old virgin adult female was presented with a gall of an adult female of *A. ovicola* collected from *Eucalyptus polyanthemos* Schauer at Chiltern-Mount Pilot National Park, Victoria. The gall contained a live adult female, as indicated by the fresh wax at the apical orifice (Fig. 4). The gall was kept at room temperature (18~24°C) before being exposed to the parasitoid. Oviposition behaviour was recorded using a Canon EOS 7D, with an attached 100 mm macro lens, as 1080p high definition video under fluorescent lighting.

In 2011, a soft, green gall of *A. ovicoloides* was collected (LGC, 8 September 2011, Higginsville, Western Australia) that contained a developing larva of *Cameronella* sp. A three-dimensional model of the wall of one quarter of the gall was constructed using sliced images with 3DMed software (http://www.mitk.net). The gall tissue was cut into 18 slices, each about 0.5 mm thick, by hand with a scalpel and both sides of each slice were photographed using an Olympus Stereo Microscope. Dark brown tracks (presumably produced by oviposition) were visible against the light yellow tissue of the gall wall. Thirty-six images of sliced gall were used to construct a 3D image in 3DMed using a "Z distance" of 14 mm. Images were enhanced for contrast and colour was inverted to show bright traces against a dark background. A stereoscopic 3D image was captured from two angles of the 3D model and aligned for parallel 3D viewing using Photoshop.

Results

After being released directly onto the gall, the wasp started antennation by walking over the gall and rapidly tapping its surface with the tips of her antennae (Fig. 3). Each time she approached the apical opening of the gall (Fig. 4) she stayed and tapped around the opening for about 5 sec (Fig. 5). Occasional preening behaviours were observed during the antennation phase. This apparent "investigating" behaviour lasted between 100-180 sec, until the female stopped midway along the gall and began drilling (Figs 6-9).

Prior to drilling, the female stopped tapping the gall with her antennal tips and moved forward such that, when the abdomen was raised and the ovipositor was placed against the gall tissue (by folding down at the junction of the first and second tergite), the tip of the ovipositor was at the place where the female had been tapping with her antennae (Fig. 6). When the tip of the ovipositor contacted the gall (Fig. 7), she separated the ovipositor

sheaths and the "dart tail" by about 30° laterally to detach the ovipositor (Fig. 8) and started to drill.

Drilling into the gall tissue appeared to involve two different movement patterns: a horizontal swinging of the abdomen combined with rapid vibration of the "dart tail" and a vertical movement. The first horizontal swinging movement consisted of a slight swing of the abdomen from side to side across an arc of about 20° at a frequency of about once every 3 sec, combined with rapid shaking of the "dart tail". After approximately 80 sec, vertical movement was added by vibrating the abdomen in the vertical plane as the legs bend and straighten to move up and down at a frequency of 2-3 times per sec. The combined movement, both horizontal and vertical, lasted about 90 sec. After that, the wasp stopped drilling for 5 seconds and then removed the ovipositor from the gall tissue by pulling it upwards (Fig. 9) and lifting it to replace it in the ovipositor sheaths (Fig. 10).

Figs 3-12. Oviposition behaviour of *Cameronella* sp.: (3) antennation; (4) apical orifice of the gall of *A. ovicola* showing wax produced by the female inside; (5) focused antennation at the apical orifice of the host; (6-8) start of drilling; (9) removing the ovipositor; (10-12) preening behaviour using hind-leg and ovipositor sheaths.

Preening behaviour was observed after the wasp removed its ovipositor from the gall tissue. The hind legs were used to brush the ovipositor (Fig. 10) and plant material adhering to the tip of the ovipositor was detached by moving the ovipositor in and out of the sheaths (Figs 11-12). After 3 mins resting and cleaning, the wasp walked away from the gall. The observed sequence of behaviours is summarised in Fig. 13.

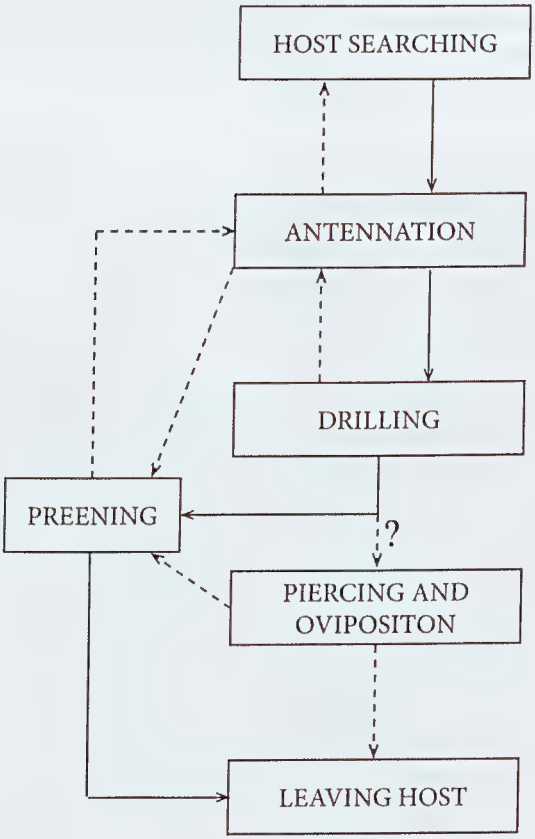

Fig. 13. Ovipositon behaviour pattern of *Cameronella* sp.: solid lines indicate the sequence of behaviours described for the last observed attempt (see text), whereas dashed lines indicate alternatives. The question mark indicates a path not observed in this study.

Four separate attempts at drilling into the gall tissue were observed. The first three each lasted no longer than 30 sec and only used the swing movement followed by further antennation, whereas the fourth attempt lasted about 170 sec. The holes drilled by the wasp during oviposition were about the same diameter as the ovipositor. It is unlikely that the wasp laid an egg during any of the four attempts because the depth to which the ovipositor penetrated was less than the thickness of the gall wall. When the gall was later opened, the scale insect was still active and showed no sign of immobilising venom having been injected. No apparent damage or other parasitoids were found on the scale insect.

The quarter of the wall of the gall of *Apiomorpha* that housed a developing larva of *Cameronella* showed signs of four attempts at drilling (Fig. 14). In two of these, the ovipositor apparently did not penetrate all the way though the gall wall, whereas in the other two attempts the ovipositor appeared to reach the inner chamber of the gall, or close to it.

Discussion

This is the first description of oviposition behaviour in *Cameronella* and in Colotrechinae. Compared with other pteromalids, the oviposition behaviour of *Cameronella* is more similar to the fig-wasp parasitoid *Apocrypta* than to *Nasonia*, in that the former two genera have not been observed to feed on host body fluids whereas females of *Nasonia* feed on haemolymph that exudes from the oviposition wound site. Here, the female of *Cameronella* did not appear to pierce the host but it is unlikely that she could feed on haemolymph given that the host is inside a gall. Most species of *Apiomorpha* are associated with ants (Gullan 1998) that, according to our observations, can stimulate the female scale insect to secrete honeydew by tapping it with their antennae. Honeydew can also be elicited from *Apiomorpha* by tickling the female with a human hair. *Cameronella* might also elicit honeydew production by tapping using their antennae, explaining the prolonged antennation at the apical orifice, but this has not been observed by the authors. Alternatively, prolonged antennation might assist the wasp in detecting the status of the potential host, for example whether it is alive and/or already parasitised. Adults of *Cameronella* likely feed on the nectar of flowers, given that a female has been netted on eucalypt flowers (collection details of E. Exley on a pin-mounted specimen in QM). Further observations are needed to test the idea that *Cameronella* might also feed on host honeydew.

The oviposition attempts reported here might have been unsuccessful because the gall of the *Apiomorpha* used for trials had become dry and hard after being picked from the tree in Victoria and transported to Brisbane, Queensland. However, the failed attempts observed in this study are apparently not rare in the field. The field-collected gall containing a developing larva of *Cameronella* showed several failed oviposition traces in

the soft walls of the gall (Fig. 14). The thickness and hardness of the gall wall could vary at different locations and it changes through the development of the gall-inducing scale insect. It is possible that females of *Cameronella* need several attempts to find a satisfactory drilling location.

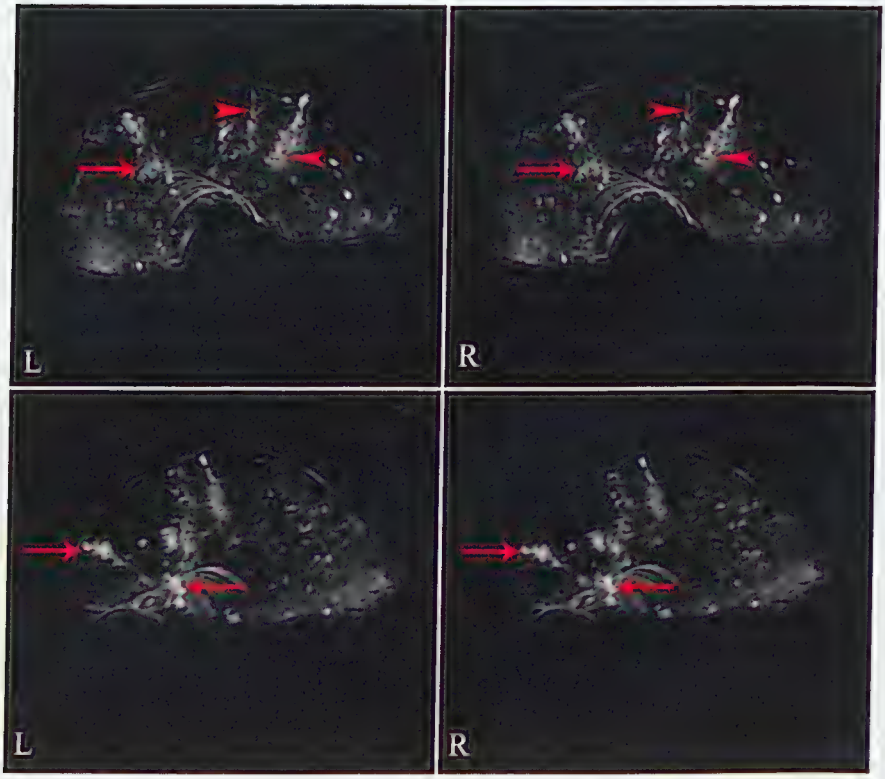

Fig. 14. Stereoscopic 3D image (parallel view) of the wall of a quarter of an *Apiomorpha* gall that housed a developing larva of *Cameronella* showing oil glands in the gall wall (bright dots) and oviposition traces (straight aligned dots). Four oviposition attempts can be observed in this part of the gall. Arrows indicate where the ovipositor appeared to reach the inner chamber of the gall, or close to it. Arrowheads indicate attempts that apparently did not penetrate all the way though the gall wall. (R: right eye view; L: left eye view; upper images: hind view; bottom images: lateral view).

Supplementary material

Videos of *Cameronella* oviposition have been edited and uploaded to http://vimeo.com/28772701 under Creative Common license of Attribution-ShareAlike 3.0 Unported (CC BY-SA 3.0).

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